THE FRUITING OF THE BLUE FLAG (IRIS VERSICOLOR L.).

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At the time of the adjournment of my college classes last June, I spent a few hours afield, watching the blue flags and their insect visitors, at first solely for the pleasant recreation that such study affords. But I soon made a few enticing little discoveries which set me to work in earnest. I began by locating all the clumps that were easy of access from my home in Lake Forest, and then I studied them daily during the flowering season, and almost daily thereafter throughout the summer.

The facts that first caught my attention were: (1) that there are many visitors to these flowers that seem to have been unnoticed hitherto; (2) that most of these are illicit visitors; and (3) that the ill-adapted ones are habitually deceived by the flower itself as to its proper entrance. I propose to give in the following pages the more important results of the season's observations.

It seemed to me that any new study of this so familiar flower should be undertaken on somewhat broader lines than are usually followed. The reproductive phase of the plant is a unit, and the flower is but one of a series of devices for furthering the reproductive process. Bud and flower and capsule and seed are the successive centers of interdependent ecological phenomena, determining the start in life of the next generation. I have tried to study the effect of insects upon the outcome of the reproductive process as a whole, and I discuss, below the chief ecological relations under the following headings: Pollination; The Waste of the Nectar; The Destruction of the Flowers; Fertilization; The Destruction of the Seeds; Inflorescence, and Chances of Maturing Fruit; The Relation of Habitat to Fertility; Alteration of Environment.

I. POLLINATION.

The flowers of the Iris have long been known to be entirely dependent on insects for the transference of their pollen. The structure of the flower has so often been described, there is no need of describing it again; if the reader has forgotten, he may refresh his memory by reference to the accompanying figures. He will recall a flower divided into three parts, requiring three separate visits by the insect which would obtain its stores; in each part an extrorse anther placed with its back against an overarching branch of the extremely large, three-parted style (Fig. 1, *R*); below anther and style a passageway to the nectary, with the usual guide streaks at its entrance, is formed by the channeled sepal. The stigma is restricted to the upper surface of an inferior, transverse, flap-like appendage of the style branch, just beyond the apex of the anther (Fig. 2). This flap is very thin and remains appressed to the style, with its free border toward the entrance, the stigmatic surface covered. The pollen-laden back of an entering insect, rubbing against it, readily everts the flap and deposits pollen on the stigmatic surface. Released, it closes

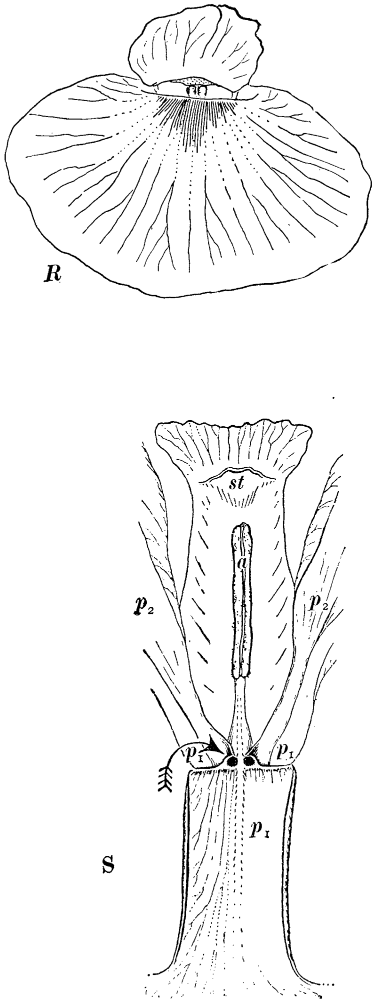


FIG. 1.—The entrance to the Iris flower, *R*, as seen from the front; parts undisturbed; *S*, as seen from the side with the sepal pulled directly downward; p_1, sepals; p_2, petals; *a.*, anther; *st.*, stigma. The arrow indicates the position of the proboscis of a pamphila when stealing the nectar.

elastically, and the rubbing of an emerging insect only closes it the more tightly.

Although the flowers are slightly protandrous, ripe pollen and fresh stigmatic surface may be found in the same flower at some period of æstivation. In case insects fail there is no provision for self-pollination by withering, as is the case in some members of the Iris family; the stigma, lifted away from the anther before maturing, remains so permanently.

I shall now discuss briefly the insects which I have seen to enter these flowers, taking them up in the order of their importance as agents of pollen distribution. I therefore begin with two small bees of closely similar size and habits: *Clisodon terminalis* Cr., *Osmia distincta* Cr.

These bees exhibit such perfection of adaptation as was the delight of the naturalists of Sprengel's day, and as will ever be delightful to observe. They were seen only in warm sunshine, during the season of abundant flowers; late and straggling flowers seemed to be neglected by them altogether. They were not the most numerous nor the most conspicuous visitors; but they visited very many flowers in rapid succession, securing the transference of the pollen with superior precision.

Each bee alights squarely at the entrance and without the slightest pause speeds down the arched passageway, and does not stop until its head is wedged in the bottom, with the proboscis extended through one of the two holes (see Fig. 1, *S*) leading to the nectary. A step backward and another momentary thrust of the proboscis, and away to another flower. That it rubs the stigma on entering may be seen by the tilting of the style tip; this is readily seen at a distance of several meters. *Osmia distincta* was perhaps a little less swift in its passage than the other, and this species alone was seen occasionally stopping on the way out from the nectary to scrape up some of the pollen fallen beneath its feet.

Next in order should be mentioned a group of syrphus flies: *Helophilus lætus* Loew.; *Syrphus torvus* O. S.; *Eristalis dimidiatus* Wied. Of these the first-named was a very common visitor. Of the other two I saw but a single specimen of each on Iris flowers, although the last-named was abundant on flowers

of the spreading dogbane. These are a little larger than *H. lætus*, and probably found the entrance way to the flower too close quarters. *H. lætus* visits the flowers for pollen only. Its proboscis is too short to reach the nectar. It wanders in at the entrance, rubbing first the stigma and then the anther with its back, swinging its proboscis from side to side, the terminal flaps sweeping the fallen pollen from the floor of the passageway. The down of its back was generally found well dusted with Iris pollen, and as an agent in pollination it was certainly second only to the bees above mentioned.

In the method of their operations these bees and syrphus flies stand in striking contrast. The bees enter and leave the flowers on the run, visiting very many in a remarkably short time; the syrphids loiter about the entrance, turning this way and that and, although entering cautiously, remain inside some time; but between visits they spend much time disporting themselves with their fellows in the sunshine. While a syrphus fly is visiting one flower a bee will visit a score.

Bombus separatus Cr. — The Iris and the bumblebee were the subjects of one of Sprengel's early studies on the relation between flowers and insects. Sprengel thought the bumblebee the only insect concerned with the fertilization of the European species (*Iris germanica*) which he studied. Müller attributed rather more importance to a very long-tongued, nectar-eating syrphid, *Rhyngia rostrata*. American writers on *Iris versicolor* have treated the bumblebee as the visitor of first importance. My observations do not corroborate this opinion. I saw but three bumblebees on Iris flowers during the entire season, and each of these was seen but a few seconds, entering from one to three flowers at one side only, and then departing. The visits were not such as bumblebees make to flowers which they habitually seek. They showed evident dissatisfaction. Indeed, they seemed to me ill-adapted. They are too large; they enter with difficulty and some delay, and crowd the stigma too roughly in passing. In the single visit which I was able to observe in detail the stigmatic flap was torn from the style for half its width; the bumblebee descended the passage with its proboscis retracted, made no

attempt at sucking, but scraped the trough of the sepal with its legs, gathering pollen.

Halictus disparilis Cr. — This minute bee is a common, though not a conspicuous nor an important visitor. It enters the flower by crawling beneath the tip of the style back downward, traverses the stigma, and walks back and forth, the length of the anther clinging to its underside, dislodging with its claws large quantities of pollen (Fig. 2). A strikingly large load of pollen is thus collected upon the hairs of its ventral surface. So it spends a long time under a single anther and visits but few in gathering its load. While it is highly probable that the bee everts and pollinates the stigma on

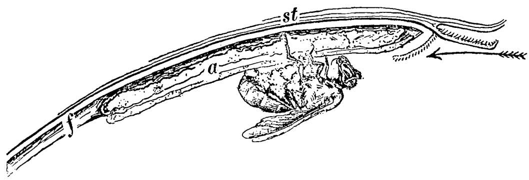


FIG. 2. — A minute bee (*Halictus disparilis* Cr ;) collecting pollen from the Iris anther; *a.*, anther. *f.*, filament; *st.*, style. The arrow indicates the course of an insect entering the flower.

entering, it is certainly very wasteful of pollen. A more equitable arrangement is seen in its relations with *Ludwigia polycarpa*, which it visits in pools near by, and whose small flowers will furnish a load of pollen only for the traversing of a multitude of stigmas.

Trichius piger Fabr. — This ubiquitous flower beetle, observed by Robertson at Carlinville in the flowers of *I. versicolor*, was rather common here. The channeled sepal seemed a favorite place for an afternoon nap. I found several there undoubtedly asleep — one so soundly that, after carrying it about in the flower in my hand for half an hour, I still had a chance to wake it. After repeatedly tickling two of its feet that were hanging over the edge of the sepal it at length stirred, then stretched itself like a lazy boy awaking; in a little while it was lively enough.

I saw one beetle in the passageway eating fallen pollen. The species is not ill-adapted by its size for visiting these flowers, and should it pass directly from flower to flower, it

might be an important agent in pollen distribution; but I have not seen one pass from flower to flower directly and am inclined to think it rarely does so. It is little disposed to flight and is much more at home clambering among the thyrsoid clusters of Rhus and Ceanothus. Furthermore, on reaching an Iris flower it is habitually deceived as to the point of entrance and tries for some time to get in at its center, between the branches of the cleft style. After clambering in and out of the central cleft repeatedly the proper entrance is at length stumbled upon. It cannot, of course, reach the nectar, and the supply of pollen on the floor of the passageway is very meager. If seeking pollen it might, if it had wit enough, get plenty of it by entering the other side up.

Mononychus vulpeculus Fabr. (*the Flag Weevil*). — This beetle is one of the most characteristic insects affecting the blue flag, and one of the commonest. It is often found in the passageway to the nectary, picking up stray pollen grains, other grains sticking to its rostrum and feet and to the scaly ventral surface of its body, but not to its smooth back. What has been said of the preceding species, as to its part in pollen transference, and as to its activities in and about the flower, will apply almost literally to this species.

Desiring to learn whether they would transfer pollen properly, and finding too few entering the flowers of their own accord, I picked up a number of them with forceps and placed them in various positions on the flowers. They all, wherever placed, ran rapidly into the central cleft of the style, seeking to enter there, climbed out, and returned to try it again repeatedly. A few then climbed out at the sides between two sepals and crawled through the space between sepal and style into the entrance way, without touching either stigma or anther. A far larger number came upon the proper entrance. Most of these latter climbed over the tip of the style and down its outer face, entering back downward, traversing both stigma and anther. A lesser number wandered out upon the tip of the sepal and returned to enter right side up; owing to the lack of pollen on their smooth backs, these would effect nothing, though they touched the stigma.

Single individuals taken from the flower again and again and replaced on top, though they sought to enter speedily, went about it in the same bungling way as before. They did not readily learn by experience.

Xylota fraudulosa Loew.; Sepsis violacea Meig; Chlorops proxima Say; C. assimilis Macq.; Chrysogaster nitida Wied. — These active little flies are minor pollen thieves, all small enough to run into the open passageway, gather a few pollen grains, and run out with them. The first is large enough to brush a low stigma in passing, and the second, a strutting, micro-hymenopter mimicker, might strike a stigma with its tilting wings; but all are very unimportant, both in pollination and in their petty thievery.

Lastly, I should not omit to mention thrips, a few of which are to be found in almost every flower, and, antithetically, a humming bird (*Trochilis colubris* Linn.) which I saw make several thrusts, in succession, with its beak into the proper entrance of these flowers.

II. The Waste of the Nectar.

Two important sources of waste of nectar were much in evidence throughout the season — lepidopters and weevils.

A. Lepidoptera. — These were, by day, skipper butterflies (Hesperidæ), and at dusk, two species of moths[1]:

Eudamus tityrus Fabr., seen at flowers several times.
Eudamus pylades Scudd., seen at flowers but once.
Pamphila hobomok Harr., seen at flowers continuously.
Pamphila peckius Kirb., seen at flowers continuously.
Pamphila cernes Bd.-Lec., seen at flowers continuously.
Pamphila mystic Scudd., seen at flowers not uncommonly.
Leucania pallens (?), seen at flowers several times.
Evergestis stramentalis, seen at flowers several times.

The pamphilas were the most conspicuous and persistent of all visitors. Throughout the season one could find at even the

[1] Another moth, *Crambus laqueatellus* Clem., was seen twice, vainly plying its proboscis at the proper entrance.

smallest clump of flowers one or more of these skippers sitting in the position shown in Pl. I, Fig. *b*, far from anther and stigma, stealing the nectar. They get it with some difficulty, to be sure, the holes opening into the nectary not being visible from the outside. They must stand outside and insert the proboscis obliquely between the sepal and the base of the style, plying and thrusting with it until a hole is found. Repeated trials occasion loss of time, and when the hole is found not all the nectar adjacent to it can be reached from one position. Nevertheless, one cannot witness the persistences of the skippers, and their abundance throughout the season, without being convinced that they get a large share of the nectar.

Very interesting as bearing on the validity of long-accepted theories of floral coloration (which some are nowadays saying were accepted without sufficient experimental proof) are the habits of the pamphilas in visiting the flowers. When the question is raised, Do the guide streaks really guide? the pamphilas on the blue flags will furnish affirmative evidence. Fig. 3 shows a flower as seen from above. The center of the flower is at the deepest point between the divisions of the style, and the lines of these divisions all point toward the center, analogously to the guide streaks on the corolla of Convolvulus. There are special guide streaks, to be sure, at the proper points of entrance; but these are in unusual places and are also arranged radiately about the center of the flower. Pamphilas visiting the flowers *habitually try to enter at the center.* One will roam over the summit of the flower, returning to try for entrance at the central cleft, again and again. When one has strayed to the end of the style branch and stumbled upon the right entrance, it will generally be seen to try for a moment to enter there. After several ineffectual attempts at the center, it will pass over the edge of the sepal and descend backward or sidewise to the position shown in the plate (Fig. *b*). That something similar was observed by Professor Charles Robertson is indicated by the two words which I have underscored in the following quotation: "Sometimes butterflies obtain nectar in an illegitimate way, by *backing down* to the base of the flower and inserting their proboscides between the bases of the

'falls' [sepals] and the style divisions."[1] He mentions *Chrysophanes thoe* Boisd. and Lec. and *Pamphila peckius* Kirb.

I have mentioned above that the flower beetle, *Trichius piger*, and the flag weevil, *Mononychus vulpeculus*, are deceived as to the proper entrance in a quite similar manner, with the difference that when these stumble upon the true entrance they can enter there. I have never seen any one of these ill-adapted visitors alight directly at the proper entrance; all fol-

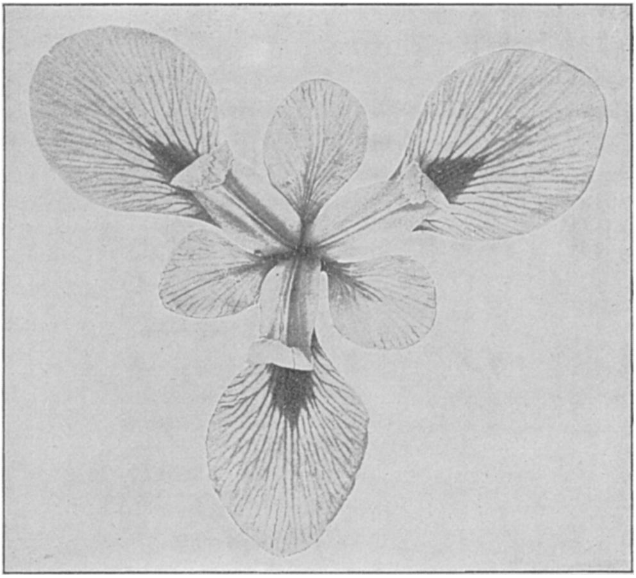


FIG. 3.—Top view of the flower; false guide streaks.

low to the center the lines simulating the guide streaks of an ordinary open flower. But the Iris flower was not evolved by these insects, nor with them. Proper visitors know where the entrance is and make no mistakes. And if the bees afore-named pass from nectary to nectary with a speed that the eye can hardly follow, must we conclude that they are not guided by the coloration of the flowers? Must we say the striking lines of violet and yellow at the entrance aid them not, because they give no sign? I think not. I may enter a barber shop guided entirely by a striped pole and yet give no sign. I

[1] Robertson, Charles. *Botanical Gazette*, vol. xxi, p. 80, 1896.

believe it an analogy which does no violence to the truth if we compare a clump of the flowers to a business block in a city. Those whose business is there go about so automatically one might think they see nothing, while strangers have to stop and read the signs; and the rapidity with which the stranger will learn to feel at home will depend, not alone upon the persistency of his presence there, but also upon his mental adaptability to such knowledge.

B. MONONYCHUS (*the Flag Weevil and its Train*). — This weevil wastes the nectar inordinately. It stands on the outside of the nectary and, with its beak, sinks a shaft into the nectariferous tissue, nibbles a little, makes another hole, and another and another, until the nectar is left flowing from many punctures, attracting swarms of insects of all sorts. One is shown in Fig. *A* of the plate, together with a number of its attendants. It is no uncommon thing to find the ovary almost covered with insects following in the wake of the weevil, collecting the sap it has set flowing. The muscids are most numerous; I have seen a weevil making a puncture with three flies facing him and one on his back, all trying to get their proboscides to the puncture, crowding one another like pigs around a trough. During hours of sunshine, competition is so keen that insects with proboscides to insert into the beetle punctures (Muscidæ, Capsidæ, Pentatomidæ, etc.) seem to have a decided advantage. I have seen the following feeding at the weevil punctures:

Muscidæ, abundant, of a number of common species.

Capsidæ, abundant, especially the first named:

Pœcilocapsus goniophorus Say, in four varieties.
Pœcilocapsus affinis Reut.
Calcoris rapidus Say.
Lygus pratensis Linn.

Pentatomidæ, very common.

Euchistus ictericus Linn.
Euchistus tristigmus Say.
Podisus spinosus Dall.

Coccinellidæ, common.

Megilla maculata DeG.
Hippodamia 13-punctata Linn.

Lampyridæ, common at dusk and on dark days, especially the first-named:

Telephorus carolinus Fabr.
Podabrus basilaris Say.
Podabrus rugulosus Lec.
Lucidota atra Fabr.

The following insects, seen more rarely :

Mordella marginata Melsh.
Prosopis affinis Smith.
Prosopis nelumbonis Robt.
Worker ant (undetermined).
Male mosquito (undetermined).

III. The Destruction of the Flowers.

The flowers of the blue flag when bitten have a sweetish taste, which seems to invite their destruction at the jaws of a number of insects that are ever near at hand. I observed adult flag weevils, noctuid moth larvæ, and grasshoppers to be especially destructive while the flowers were in full bloom.[1] Any service the weevils may render as pollinators is greatly overbalanced by the destructiveness of their feeding habits. Not content with puncturing the walls of the nectary, they sometimes riddle the perianth leaves and the style divisions, destroying or (what is equally fatal) displacing the parts concerned in fertilization.[2]

All the grasshoppers (Acrididæ and Locustidæ) about the flag beds and in the neighboring sedges eat the freshly opened flowers, mainly nibbling a little at the margins of the petals or sepals and doing little real harm, but sometimes destroying the flowers completely.

The destructive moth larvæ were of three species : *Arsilonche albovenosa* Goeze, Mamestra *sp.* ?[3] and *Spilosoma con-*

[1] Feeding upon the wilted flowers a day after they had closed and when their sap was souring were frequently observed the three following beetles : *Trichodes nuttalli* Kirb. ; *Megilla maculata* DeG. ; and *Telephorus carolinus* Fabr.

[2] This weevil has been reported by Mr. G. C. Davis as very destructive to imported garden Irides, at Flint, Mich. *Insect Life*, vol. vii, p. 201, 1894.

[3] I did not rear this species; two of my larvæ taken for rearing were parasitized with a species of Apanteles; the remainder (as well as many in the field) died of some bacterial disease. *Arsilonche albovenosa* was abundantly parasitized with *Rhogas intermedius* Cr.

grua Walk. At the time the Iris flowers opened, these larvæ were well grown. They then forsook the leaves, on which they had been feeding hitherto, for the daintier floral diet.

Chætopsis ænea Wied. and its Train. — This little bud-destroying ortalid fly deserves special mention, because in certain situations it does more to prevent fruiting than all other insect enemies combined. Furthermore, its attack comes earliest; its larva enters the pedicel at the base of the flower bud and bores downward into the common flowering stem (peduncle), killing not one bud, but the cluster of two or three arising at that point. Thus the flowers are killed before they open and are left to decay.

Walking through a pasture near Lake Bluff, Ill., one day, I was led to examine some large clumps of flags by the very bad odor of their Chætopsis-killed flowers. In clumps of several hundred plants each, not a single flower had been permitted to open. Finding Chætopsis larvæ still present in some of the pedicels, I collected a hundred or more terminal branches of the flower clusters and placed them on end in a jar, with a little water, some gravel, earth, etc., in the bottom, covered the jar with fine netting, and set it aside to await developments.

My little jar yielded, not a single species, but a little community — a succession of interdependent forms, such as one often finds among insects with a brief life history, able to take advantage of a transient food supply. First there appeared a number of pomace flies (*Drosophila phalerata* Meig), which had probably been attracted to the buds by the souring of their saccharine juices. Next appeared the ortalids (*Chætopsis ænea* Wied.), the cause of all the trouble. These I found left the stems when full-grown larvæ and pupated on the wet soil in the bottom of the jar. By this time the rotting buds were teeming with oscinid larvæ and studded all over the outside with pupæ, from which soon issued swarms of the minute fly, *Oscinis soror* Macq. With these also appeared a small number of beetles (undetermined) and a few parasitic Hymenoptera (*Spalangia drosophilæ* Ashm. and Heptamerocera *sp.* ?). Finally, after the decaying buds had been completely overrun with mycelial

threads of fungus, there appeared fungus gnats (*Scatopse pulicaria* Loew.) in great numbers. It is quite probable that the ortalids attacking the fresh buds, the pomace flies coming when the saccharine juices of the flower first begin to ferment, the other flies and beetles clearing up the rotting débris, with a few parasites to hold the commonest in check, form an entirely natural succession of forms belonging with such conditions.

IV. Fertilization.

Not wishing to leave actual fertilization out of account, I (1) pollinated by hand a large number of flowers and marked them for examination later, and (2) counted the fertile and abortive ovules in a large number of capsules developing from flowers fertilized by insects. In my hand-pollination experiment half the flowers were treated with their own pollen, half with pollen from other plants. Before the seeds had grown sufficiently to be distinguished with certainty from the abortive ovules, grasshoppers and Mamestra larvæ had eaten all but a few. Those that remained happened to be half self-pollinated, half cross-pollinated, and the result may be worth mentioning, even though they were but few. The average by capsules was as follows:

Cross-pollinated,	ovules, 79;	fertilized, 74,	unfertilized,	5 (for 2 capsules).
Self	" " 82;	" 16,	"	66 (" 2 ").

These were small capsules, from flags growing among thick sedges.

In a flourishing flag clump growing in the edge of a woodland pool I selected thirty well-developed capsules from flowers fertilized by insects, for the following tabulation. The position of the several capsules in the cluster is indicated by the lettering in the first column, which is the same as that of Fig. 4.

TABLE I. — AVERAGES OF FERTILIZATION BY INSECTS FOR 30 CAPSULES.

CAPSULES.	AVERAGE NUMBER OF OVULES.	FERTILIZED.	UNFERTILIZED.	PER CENT FERTILIZED.	NUMBER OF CAPSULES COUNTED.
I *a*	126	74	52	58.73	10
I *b*	129	57	72	44.96	5
I *c*	114	32	82	28.07	5
II *a*	123	44	79	35.77	5
II *b*	113	40	73	35.39	5
Totals	122	43	68	43	30

V. THE DESTRUCTION OF THE SEEDS.

I observed two types of seed destroyers, ecologically speaking: (1) those which are locally destructive, and (2) those which are with the flag in all the situations in which it grows. The influence of situation will be discussed under a subsequent heading, but here may be mentioned the insects locally destructive to the developing seeds. These are grasshoppers, Mamestra larvæ, and ovipositing damsel flies of the genus Lestes.

The grasshoppers are very destructive in meadow clumps and in the drier, more grassy situations, sometimes eating all the capsules over considerable areas, while generally disdaining to eat the leaves at all.

Of the three moth larvæ already mentioned as feeding on the flowers, only Mamestra remains to attack the developing ovary; the others return to their aforetime diet of leaves. But Mamestra, having once bitten into a juicy capsule, will eat nothing else thereafter, so long as capsules are obtainable. In my rearing cages a single larva would eat out all the seeds from a well-grown capsule in two days. Mamestra hardly comes into competition with the grasshoppers, since it avoids the drier situations where these are numerous enough to be destructive.

The injury from Lestes was still more local and was of a sort apparently not hitherto recorded. It was confined to flags

growing in standing water. The sheltered pools in which the Iris thrives best are the special haunts of these insects. *Lestes uncata* Kirby and *L. unguiculata* Hag. were abundant, and the females of these species punctured the fruiting stems so thickly in ovipositing as to kill perhaps a fourth of them. These egg punctures sometimes completely encircled the stem, but were more often confined to the more exposed side, overhanging the water. I observed as many as 250 punctures to the inch in length of stem in several cases. All were above water, some extending nearly to the top of the stems.[1] Nearly every well-exposed stem was thus killed outright or so injured as to prevent the maturing of its seeds.

Many other Odonata are seen constantly about the flag clumps. Longfellow singled out a natural associate when he wrote of the Fleur-de-lis:

> The burnished dragonfly is thine attendant;

but the showier dragonflies which habitually poise on the summits of the sword-shaped leaves have no ecologic relation to the Iris, save indirectly through their relations with other insects.

Of ubiquitous flag-seed destroyers I have found but two; the larvæ of a very pretty little tortricid moth, *Penthina hebesana* Walk., and the larvæ of the flag weevil (*Mononychus vulpeculus* Fabr.). The moth larvæ were common, the weevil larvæ, abundant; both were often found attacking the same capsule.

The larva of Penthina bores a hole into the seed capsule at its base, generally under the protecting tip of a bract, and eats its way upward through the seeds, usually consuming in its lifetime about half the contents of a single cell. Then it undergoes its transformations under the bract, or withered perianth, or in its burrow.[2]

[1] Egg parasites of Odonata have not in this country been hitherto reported; I bred from these Lestes eggs in flag stems five species of egg parasites and one hyperparasite, all of which proved to be species new to science. These are now in Mr. Ashmead's hands for description. These species of Lestes oviposit even more abundantly in Spharganium leaves.

[2] With this species there was occasionally found another tortricid (*Cacœcia rosaceana* Harris) of almost identical habits.

The flag weevil (*Mononychus vulpeculus* Fabr.) has already been mentioned as a denizen and, to some extent, a destroyer of Iris flowers. The height of the season for the adult weevils is the blossoming time of the flowers. Even then they are not very active; I have found them flying freely from clump to clump only in the hot sunshine of early afternoon. They will dodge around the base of the flower like a squirrel around a branch when a hand approaches, but they will rarely fly; they will oftener fall to the earth or into the water. The females when ovipositing are still more shy and difficult to observe. I was able to see the details of the process of egg laying on only one day — a very windy day, when everything about the weevil was in motion, and my own movements were, therefore, less noticed. The mother beetle rapidly gnaws a little hole through the wall of the ovary and, taking a few steps forward, inserts an egg into it. She then walks a little way and repeats the process or gnaws aimless little pits over the surface of the ovary.[1] The wounds thus made are quickly stopped by the discharge from mucilage cells, which are abundant in the walls of the ovary. The egg is often inserted into the external face of an ovule.

When the egg hatches, the larva at once begins a shallow furrow across the outer ends of the developing seeds, traversing from two to ten of them. Thus it spends the larger part of its larval life, doing no damage whatever. In fact, during this stage it is in considerable danger of being eaten, along with the seeds, by grasshoppers or Mamestra larvæ. Entering upon its last larval stage, the larva burrows downward and begins feeding on the softer tissues of the center of the seeds. It eats voraciously and grows with marked rapidity. It burrows parallel with the axis of the capsule through the center of from three to five seeds, leaving of them only empty rings. Its growth is completed and all its damage is done during this stage, which lasts only about a week. Then it transforms

[1] Possibly these blind pits may serve for the confusion of the weevil's parasites. I found a little egg, presumably that of a parasite, just within the entrance to a hole, at the bottom of which a weevil egg was lying. Mr. J. Hamilton found the parasites (*Ent. News*, vol. v, pp. 287, 288, 1894).

within its burrow and remains there as an imago, until the bursting of the capsules in autumn causes the seeds and the weevils to be shed together.

To determine the extent of the damage done by the weevil to the flag seeds, I picked at random, in several situations, fifty well-developed capsules and counted the weevils in them. The result by capsules was as follows:

Number of larvæ per capsule,	0,	1,	2,	3,	4,	5,	6,	7,	8,	9,	10,	12,	15,	16.
Number of times occurring,	3,	2,	4,	8,	4,	11,	3,	6,	1,	1,	2,	1,	1,	1.

Thus, but three were found without larvæ in them; two contained such numbers (fifteen and sixteen, respectively) that there were hardly enough seeds to insure their development; the total number of larvæ was 269, the average number per capsule, five. Each larva destroys on an average about four seeds; a preceding table has shown that the average number of seeds developing per capsule (among thirty counted) was forty-three. So it appeared that the weevils destroyed nearly half the seeds in capsules which had escaped other destroyers, all of which had had their turn first.

While this weevil is the most constant enemy of the blue flag, it is at the same time the one best regulated. Unlike other enemies, it is present on or in the plant throughout the season, and, though occurring everywhere, it is never wholly destructive anywhere. Its own habits furnish checks to too great multiplication. This is but saying that the weevil represents a higher type of ecologic specialization. It has become adapted for living on the blue flag exclusively. Other enemies might totally devastate the flag clumps and, in the next generation, turn to some other food plant; but excessive injury by the weevil means future starvation for its kind. The grasshoppers, Mamestra and Chætopsis, work a havoc that strikingly suggests a disturbance of the balance of nature. But the weevil goes its accustomed way — the way into which it has been led by natural selection — and gets its living unobtrusively; and save for the rather rare damage to flowers, which may as often be done after fertilization as before, the flags show no visible sign of the burden which, under natural conditions, they are doubtless able to carry.

VI. Inflorescence, and Chances of Maturing Fruit.

The flowering stem of *I. versicolor* bears a terminal cluster of three flowers and generally one or more lateral clusters of two flowers [1] each, the latter springing from the axils of alternating bracts. Fig. 4 represents a stem which bore the typical complement of flowers. For convenience of reference I designate these clusters by the Roman numerals applied to them in the figure. Cluster *I* is developed in all (100 per cent); cluster *II*, in about 60 per cent of the stems; cluster *III*, in about 10 per cent of them; and cluster *IV* is rarely developed; I found it but once during the season.[2] The small letters indicate the several flowers in the clusters and also the order of their opening. The clusters are nearly isochronous, but there is some irregularity. Flower *I a* is generally the first to open. The few flowers which I marked for observation opened in the morning before nine o'clock, and closed by withering during the afternoon of the day following. Flowers *a, b,* and *c* follow each other in regular succession, each being

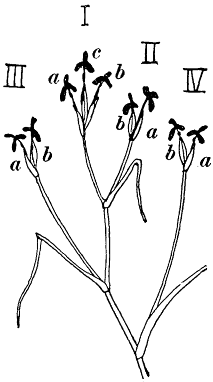


FIG. 4. — Diagram of the flower cluster.

[1] The statement of Goodale (*Wild Flowers of North America*, p. 32, 1882) that "the flowers may be single or in clusters of two, rarely more" is certainly not true for the vicinity of Lake Forest; I found but a single clump to which it would at all apply — a clump of much-dwarfed plants growing on a very dry hillock in a pasture near Fort Sheridan. This singular clump bore twenty flowering stems, of which five had cluster *I* only, with but two flowers (*a* and *b*) in that cluster; twelve had clusters *I* and *II* developed, with the second flower (*b*) developed in *II* but twice; and three with clusters *I, II,* and *III* developed, and only one flower (*a*) present in cluster *III.* Elsewhere I found three examples of cluster *I* in which a fourth flower (*d*) was developed, and two in which the third flower (*c*) was not developed. The usual four bracts were developed in all; but the terminal bract, usually sterile, was fertile in three, and the third bract, usually fertile, was sterile in the other two. I also found a single cluster *II* containing three flowers.

[2] These percentages were derived from a count of 214 stems — the same ones which were used in drawing up Table II. A subsequent count of 129 stems from other localities near Lake Forest yielded slightly different results, as follows: cluster *I* developed in all (100 per cent); cluster *II* developed in 87 (67.5 per cent); cluster *III* developed in 21 (16.3 per cent).

open for two days. Sometimes there is an interval of a day or two with no flower open. Some striking differences in time of flowering, due to situation, will be noticed under the next heading.

I collected 214 stems from five different localities and studied them to determine the proportionate fertility of the several capsules. Wholly infertile stems I disregarded altogether, and capsules developing any seed at all I counted fertile; Table II summarizes the results of the count. Disregarding localities for the present, the total percentages of fertility are as follows:

Flower	*I a*, 75 per cent;	*I b*, 63 per cent;	I *c*, 28 per cent.
"	*II a*, 66 per cent;	*II b*, 43 per cent.	
"	*III a*, 68 per cent;	*III b*, 54 per cent.[1]	

Clearly, the advantage is with the earlier flowers.

But is there not further significance in these facts? In connection with the occasional occurrence of an extra flower in clusters *I* and *II* they seem to me to suggest that the flower cluster is in process of reduction by elimination of the later flowers. The observations of one season will not determine such a matter. It is sufficient to record the conditions of the present, that the future student may have the criteria necessary for determining it.

VII. The Relation of Habitat to Fertility.

My observations were all made on the eastern slope of the narrow Lake Forest moraine, which forms a part of the west shore of Lake Michigan, its wave-worn eastern edge rising abruptly some seventy feet from the water. Numerous sharp, post-glacial ravines, whose puny streams take their origin among the pools, marshes, and "potholes" of the crest of the moraine and reach the lake level only at their mouths, give considerable variety to the otherwise uniform and scarcely perceptible eastward slope. I found and studied the blue flag growing in eight different sorts of situations. These will be referred to by numbers in the succeeding tables, as follows:

[1] The higher percentages for cluster *III* are somewhat misleading, because this cluster is developed only under the most favorable conditions.

Locality 1. — A small clump of perhaps fifteen plants, growing in the edge of a little creek that was formed by the confluence of a number of ravines, near the lake and almost at the lake level. But one clump was found in this situation, and it bore but fourteen flowering stems; but, because of its striking vigor, fertility, and comparative exemption from insect enemies, it is included in the table.

Locality 2. — A large area of flags, growing in an upland meadow pool that was the head water of one branch of the forementioned creek. This was the most extensive and the most typical of the clumps studied.

Locality 3. — A large and compact clump, growing in the edge of a woodland pool.

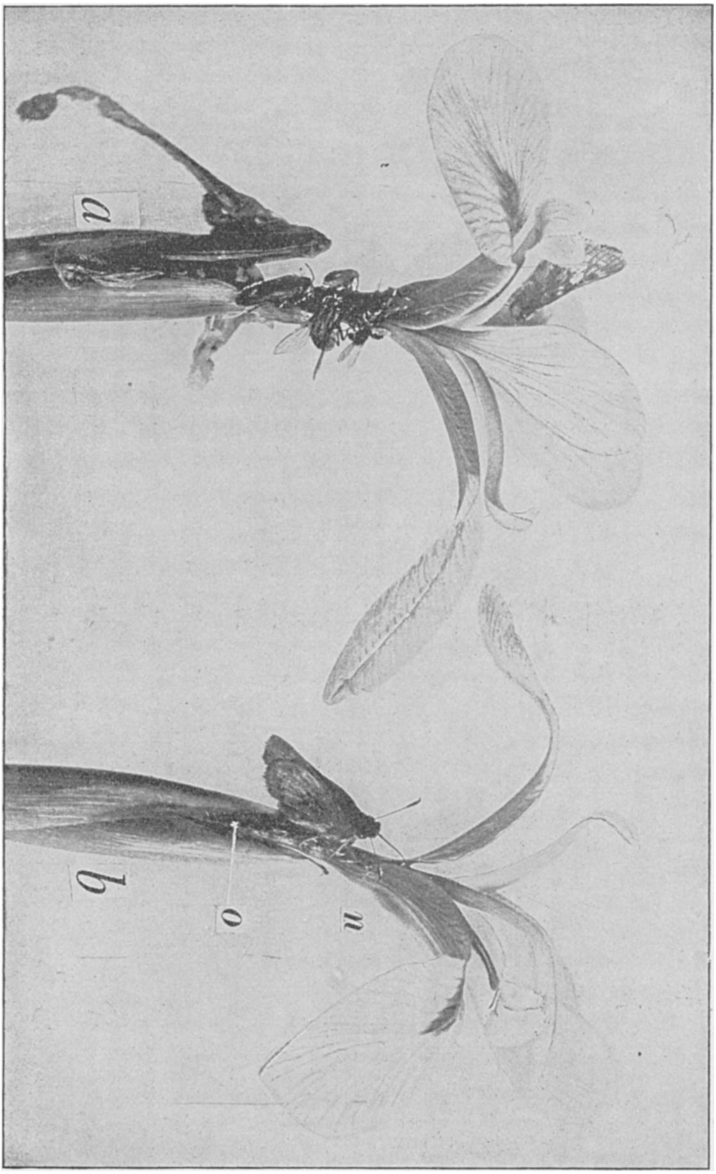
Locality 4. — Isolated single plants, growing between the sedges and the open water in a woodland pool.

Locality 5. — A large number of scattered plants, growing among the sedges of a "filled-in" pool.

Locality 6. — A typical glacial "pothole" in deep woods on the summit of the moraine, with abrupt banks, some depth of water in the middle, closely bordered with great oaks, and almost filled with a dense growth of buttonbush (Cephalanthus). The flags grew between the buttonbush hummocks and the shore, tall and spindling, with remarkably pale flowers. They bloomed late, the water of the pothole being rather cold, and, with the exception of two flowering stems which grew upon an unoccupied hummock, set no seed at all; hence this locality is omitted from Table II.

Locality 7. — At the foot of a hill bordering the creek mentioned above (locality 1), in a pool of cold water, the outflow from a spring, grew perhaps fifty plants, intermixed with cattails and sedges. These made a very promising appearance, but they bloomed late; the flowers were considerably damaged by weevils and set little seed, and that little was early destroyed and none left for tabulation.

Locality 8. — In a bottom-land pasture bordering the creek numerous large, apparently healthy, clumps on dry ground. This ground had once been marshy bottom land; but as a result of pasturage, tillage, and deforestation of the hills above floods



Pl. I. — Two Iris flowers, with some illicit visitors. Entering the cleft in the style of flower *a*, *Pamphila peckius* Kirb.; on the left side of the nectary, a flag weevil (*Mononychus vulpeculus* Fabr.) surrounded by a group of Muscidæ; below, a lampyrid (*Telephorus carolinus* Fabr.), also seeking nectar. On flower *b*, *Pamphila cernes* Bd.-Lec. stealing the nectar; *n.*, nectary; *o.*, ovary. This, and Fig. 3, photographed from life by the author.

had increased, and the creek had deepened its channel, leaving the flag clumps high and dry. The flowers were destroyed by Chætopsis, setting no seed at all.

Thus, only the five first-named localities were available for the following tabulation.

TABLE II. — COMPILATION OF DATA ON IRIS FRUITING.

			Capsules Fertile.								By Clusters.				
Clusters.	From	No.	*a.*	*Percentage.*	*b.*	*Percentage.*	*c.*	*Percentage.*	*Total.*	*Percentage.*	*All Abortive.*	*Both a and b Fertile.*	*Percentage.*	*a, b, and c Fertile.*	*Percentage.*
I	loc. 1	14	10		9		9		28	66%	0	8	57%	7	50%
	" 2	125	95		81		36		212	57%	0	74	59%	34	27%
	" 3	25	18		20		8		46	63%	0	13	52%	3	16%
	" 4	25	21		18		6		45	63%	1	16	64%	6	25%
	" 5	25	17		7		2		26	35%	0	7	28%	1	4%
	Total	214	161	75%	135	63%	61	28%	357	56%	1	118	55%	51	24%
II	loc. 1	10	7		4				11	55%	0	4	40%		
	" 2	75	56		39				95	63%	2	38	50%		
	" 3	15	10		7				17	57%	4	6	40%		
	" 4	13	8		5				13	50%	3	4	34%		
	" 5	15	3		0				3	10%	12	0			
	Total	128	84	66%	55	43%			139	54%	21	52	41%		
III	loc. 1	7	5		6				11	79%	0	5	71%		
	" 2	12	8		4				12	50%	0	3	25%		
	" 3	1	1		1				2	100%	0	1	100%		
	" 4	1	1		1				2	100%	0	1	100%		
	" 5	1	0		0				0		1	0			
	Total	22	15	68%	12	54%			27	61%	1	10	45%		
IV	A single example from loc. 1, both capsules fertile.														

This study by localities shows that the flags which grow in shallow water with open exposure to the sun have the better of it. Doubtless this but indicates their natural habitat.

The inference previously drawn from this table, that the earlier flowers have the advantage, is strikingly corroborated

by the study of localities 6 and 7, in which cold water and consequent late flowering are accompanied by nearly total infertility. While various reasons might be assigned for this advantage, I am inclined to believe that the principal reason is the coincidence of the visits of the bees, pollen distributers *par excellence*, with the time of blossoming of the early flowers.

The following table expresses in general terms the relation which ravage by insect enemies was seen to bear to situation. The first three columns express broadly the more potent features of the several situations. In six columns are indicated, by abbreviations of their respective scientific names, the six chief insect enemies: Mononychus, Penthina, Mamestra, Arsilonche, Orthoptera (grasshoppers), and Chætopsis; the numbers in these columns merely indicate the relative destructiveness of the insects named for each locality. In the last column is given the percentage of injury done by the species that was most destructive in each locality.

TABLE III. — RELATION OF INSECT RAVAGE TO IRIS HABITAT.

Loc.	Exposure to Sun.	Water.		Insect Enemies.						Highest Percentage of Injury.
		Amount.	*Temperature.*	*Mon.*	*Pen.*	*Mam.*	*Ars.*	*Orth.*	*Chæ.*	
1	Open	6 inches	Warm	3	4	1		2		10
2	"	1–6 "	"	2	3	1	5	4	6	30
3	"	4 "	"	3	4	1	6	2	5	40
4	"	6 "	"	3	4	1	2	5	6	60
5	Overtopping sedges	Wet soil		5	6	2	3	1	4	60
6	Deeply shaded	0–20 inches	Cold	1						45
7	Open	0–4 "	Cold (spring)	1	4	3		2	5	50
8	"	Moist soil							1	100

So the blue flag is growing in certain native habitats now, under altered conditions, apparently not normal to it, in which it meets with enemies against which it is not fitted to cope.

VIII. Alteration of Environment.

The blue flag has been less disturbed by the progress of civilization than most native species. Wild trees and shrubs and flowers have been uprooted, and cereals and forage crops planted in their place, for the farmer coveted their fields. But the Iris grows in wet places, not at once available for tillage. Yet it has suffered, both directly and indirectly; directly, through artificial drainage, drying up its native shoals; indirectly, through the influence of the change upon insects affecting its life history. It would be worth much to know, for the sake of comparison, what its relations to insects were before the white man came. In the absence of such certain knowledge there are facts of ecological adaptation which may justify an opinion as to some results of the change. To "civilization" I am inclined to attribute the following phenomena:

1. *The Destructive Abundance of Chætopsis ænea Wied.* — This species is an habitual enemy of the coarser, succulent grasses and cereal grains,[1] boring in their stems. Successive broods could not be maintained on the Iris, but the cultivation of corn and oats affords it almost unlimited opportunities for multiplication. A neighboring cornfield of the preceding year may well have furnished the swarms that devastated the Iris in locality 8. The scattering growth of the native coarser grasses in this region would not be likely to yield such swarms any season.

2. *The Injury locally wrought by the Grasshoppers.* — These were all field and meadow loving species, such as have doubtless become much more numerous in this region since the cultivation of their food plants was begun. Partial drainage, bringing the forage grasses and the flag clumps into closer proximity, would encourage the attack.

3. *The Nectar-Stealing of the Pamphilas.* — The constant presence of large numbers of these butterflies, so well adapted for another type of flower, upon the Iris, which is so well adapted to another type of insect, furnishes an example of

[1] *Vide* Howard, L. O. An Ortalid Fly Injuring Growing Cereals, *Insect Life*, vol. vii, pp. 352–354 (Fig.), 1895.

marked unfitness where nature generally shows the finest adaptations. "Civilization" may well be held responsible for this. The larvæ of the pamphilas feed on grass, and meadows and pastures have greatly increased the amount of grass available for their food. The butterflies, on the contrary, feed only on the nectar of wild flowers; these have correspondingly diminished in number; and the supply of nectar available for so specialized an insect has become very scant. They visit the Iris, because "stern necessity compels." They are equally abundant about the flowers of *Geranium maculatum* Linn., which blooms at the same time, and about every other species from which they can get any nectar. Were enough nectar available in flowers adapted to them, I think it quite likely that they would leave the Iris flowers unmolested.

I could not satisfy myself as to whether the apparent scarcity of the finely adapted bees (the only insects for which the nectar of the blue flag is made entirely available) was due to the diminishing of the nectar stores by the pamphilas or to some more remote cause effecting a decimation in the actual number of bees. But they were few about the flowers at the most favorable times; and the foregoing tables have shown the ovules incompletely fertilized.

I trust I have shown in the foregoing pages that the flower should be studied as only one factor in the reproductive process, its pollination, one of the links in the chain of circumstances, binding together two generations. It should be studied (1) in relation to local fauna and flora, (2) in relation to latitude, season, and situation, and (3) in relation to changing conditions of environment. Past studies of flowers and insects, though very numerous, are only complete in having completely demonstrated the interdependence of these and in having shown the existence of numerous coadaptations between them. There are broader ecological adaptations yet to be worked out, which may explain the fitting of a species to its place in natural society, but which will certainly require the coöperation of students, in various places and for a long time, content to spend much labor in gathering and correlating ecological data.

NOTE. — For help generously given me in the determination of the names of the insects mentioned in the foregoing paper I am indebted to a number of gentlemen, as follows: Coleoptera, Mr. Samuel Henshaw; Microlepidoptera, Professor C. H. Fernald; other moths, Professor John B. Smith; Hesperidæ, Mr. John Healy; Apinæ, Professor Charles Robertson; and, through the kindness of Dr. L. O. Howard, the following from the division of entomology of the Department of Agriculture: Hymenoptera, Mr. W. H. Ashmead; Diptera, Mr. D. W. Coquillett; Hemiptera, Mr. O. Heidemann.